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STRUCTURE, MOVEMENTS AND REPRODUCTION IN THREE COSTA RICAN BAT COMMUNITIES

By

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The ecological role of bats in tropical forest communities has only recently come to be appreciated by biologists and is still far from being fully documented or evaluated. In Costa Rica, varied physiography results in drastically changing rainfall and temperature regimes and consequently, a diversity of different floral and faunal communities within a relatively small geographical area. The adaptive patterns within bat communities to these various associations are of great interest in view of the important involvements of bats as insect predators, seed disseminators and pollinators within tropical communities.

Ecological investigations of Neotropical bats, especially in Costa Rica, have greatly enhanced our knowledge of chiropteran biology and distribution there. Recent contributions include Gardner, et al. (1970), LaVal (1970), Fleming, et al. (1972), and Heithaus, et al. (1975). From February 1973 through March 1974 we gathered data on several of the most common frugivorous and insectivorous species of bats at three sites in Costa Rica. Data were obtained for 78 of the approximately 100 species of bats known to occur in Costa Rica.

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Materials and Methods

Objectives and Techniques.—This study is a segment of a larger project, the objectives of which were to correlate seasonal cycles in the reproduction, food habits, and behavior of Neotropical insect predators with environmental cycles as reflected by plant phenology and changes in prey abundance. In the present paper, we have attempted to resolve the following questions: How are bats distributed among three major habitats at our study sites? How does community structure at three sites of contrasting climate and vegetation differ as indicated by diversity indices and niche matrices based on size and feeding behavior? How far do bats move in their foraging activities, and how are these movements related to food habits and to the real size of activity ranges? Finally, to what extent are seasonal climatic changes reflected in the reproductive strategies of bats?

Data were obtained from three sites in Costa Rica—La Selva, Monteverde and La Pacifica. Ten- and 14-meter mist nets and 1.7 m × 1.5 m harp traps (Tuttle, 1974a) were erected to block trails through undisturbed forest, second growth forest, and plantations of bananas, coffee, palms, and cacao. The traps were in regular use only at La Selva and Monteverde. Mark, release, and recapture techniques were employed, using the metal or plastic bat bands issued by the National Fish and Wildlife Laboratory or purchased from A. C. Hughes, Hampton Hill, England.

At La Selva, nets were set in a different location on each night of sampling. Netting activity was alternated between the western and eastern halves of the area, with distances of up to 2300 m between netting sites. The trap was erected on the same trails, but usually on the half of the area opposite the half where the nets were set. Owing to the patchwork character of the forest, coverage at Monteverde was spotty. Most of the netting sites were clumped within a circle of one kilometer diameter. The greatest distance between any two sites was 1500 m. Our data from La Pacifica, COMELCO, and other sites in Guanacaste do not lend themselves to the elucidation of movement patterns.

During the study period 1184 bats of 52 species (excluding *Molossus sinaloae* at a roost site) were banded at La Selva, and 613 bats of 20 species were banded at Monteverde. An additional 678 individuals of 35 species were captured in Guanacaste.

The biases inherent in some of these techniques were discussed by LaVal (1970) and Fleming, et al. (1972). Use of the harp trap in the tropics has been mentioned only briefly in the literature (Tuttle, 1974b). The trap was designed specifically to catch bats of the genus *Myotis* (M. D. Tuttle, pers. comm.) but is effective for a variety of other small bats up to the size of *Carollia brevicauda*

(15-20 g). Larger bats such as *Trachops cirrhosus* (30-40 g) and *Artibeus jamaicensis* (40-60 g) seldom were caught. Some of the species trapped apparently were adept at avoiding mist nets and thus have been poorly represented in previous studies. For example, *Myotis riparius* (La Selva) and *Myotis keaysi* (Monteverde) were among the bats caught most commonly in the trap, but they rarely have been taken in mist nets. Though not effective in heavy rain, the trap seems to be superior to mist nets in light rain because mist nets eventually become waterlogged, resulting in a decline in catch-rate.

Bats also were captured in a variety of other ways, mostly by hand in hollow logs and trees. Several species were caught only in a mist net set outside a *Molossus sinaloae* roost in a building, and another building served occasionally as a roost for two species of *Myotis*.

Bats were preserved in alcohol when specimens were needed to confirm field identifications or to examine reproductive tracts, and are deposited in the Museum of Natural History, The University of Kansas. All other individuals captured were released after recording sex, age class (juvenile, subadult, adult), reproductive condition, forearm length and weight. Fecal samples containing insect remains or seeds were retained.

The names used for bat species follow Hall and Kelson (1959) except in cases where more recent taxonomic revisions exist. At La Selva, the three species of *Carollia* with which Fleming, et al. (1972) encountered difficulty in Panamá (*castanea, brevicauda* and *perspicillata*) can be readily separated in the field (see Pine, 1972). Also at La Selva, *Myotis riparius* and *M. elegans* broadly overlap in several external characters that supposedly separate them (see LaVal, 1973), and we could find no one set of characters that would ensure correct field identifications. The best single character (often requiring the use of a hand lens) is the relatively crowded condition of the small upper premolars in *M. riparius*. *Artibeus phaeotis* and *A. watsoni* at La Selva appear identical externally. The individuals lacking the third molars were identified as *A. phaeotis* and those having them as *A. watsoni*, following Davis (1969). *Hylonycteris underwoodi* and *Choeroniscus godmani* were difficult to separate at La Selva and Monteverde, but the bicolored fur of *Choeroniscus* usually distinguished it from *Hylonycteris*, which has tricolored fur. At Monteverde all small *Artibeus* were identified as *A. toltecus*. Although there is a possibility that a few were actually of the very similar species, *A. aztecus*, all preserved examples proved to be *A. toltecus*.

Study Areas.—The three study sites are characterized by contrasting climate and vegetation: La Selva, *ca.* 100 m elevation, Tropical Wet Forest (Holdridge, 1967), in the Caribbean lowlands;

Monteverde, 1400-1600 m elevation, Premontane Moist and Premontane Wet forests, on the Pacific slope of the Cordillera de Tileran; La Pacifica, COMELCO Ranch, and nearby sites, *ca.* 100 m elevation, Tropical Dry Forest, in the Pacific lowlands of Guanacaste Province. The La Selva site has been described by Orians (1969, and see references in Fleming, 1974), and the La Pacifica site by Fleming (1974). La Selva and COMELCO were described by Frankie, et al. (1974). Monteverde is a dairy-farming community on moderately-sloping terrain near the continental divide. Pastures typically are separated by strips or tracts of forest, mostly undisturbed, amounting to about 30 percent of the total land area. The community is bordered on two sides by the Monteverde Cloud Forest Preserve and the Monteverde watershed, which together constitute about 1551 hectares of continuous, undisturbed forest. The dessicating effects of the harsh Pacific dry season are moderated by low temperatures (Table 1), higher rainfall (Fig. 1), cloud cover, and mists blown over the divide from the wet Caribbean slopes (see also Rentz, 1975). As a result, the forest is largely evergreen and supports many faunal and floral elements more typical of the Caribbean slopes and lowlands. The remainder of the biota consists of a mixture of montane species, species characteristic of the Pacific lowlands, and species of wide altitudinal range.

Netting and trapping were carried out in or near undisturbed forest at La Selva, in both disturbed and undisturbed forest at Monteverde, and in riparian forest at La Pacifica and at the nearby COMELCO Ranch. Nets and traps were set at ground level across trails. In the La Pacifica area, netting efforts were concentrated on a few insectivorous species because of the extensive amount of data already compiled there on other species by Fleming, et al. (1972) and LaVal (1970).

At all localities, netting and trapping periods were confined to about eight to ten nights a month, with the trap set each night but the nets only on the most favorable nights. Scheduling problems and periods of unfavorable weather reduced the actual number of sampling periods to ten at each site.

TABLE 1.—Temperature (°C) and Rainfall (mm) at Three Sites in Costa Rica from Records of the Costa Rican Meteorological Service; Ranges Given in Parentheses.

	La Selva	Monteverde	La Pacifica
$\bar{X}$ monthly temperature	24.1(22.8-24.9)	14.9(14.1-15.6)	27.8(26.2-29.0)
$\bar{X}$ annual rainfall	3961(2921-5659)	2482(1716-3180)	1528(959-2267)
Months of dry season	Feb.-Mar.	Jan.-Apr.	Dec.-Apr.
$\bar{X}$ monthly rainfall during dry season	172.5	47.5	21.3

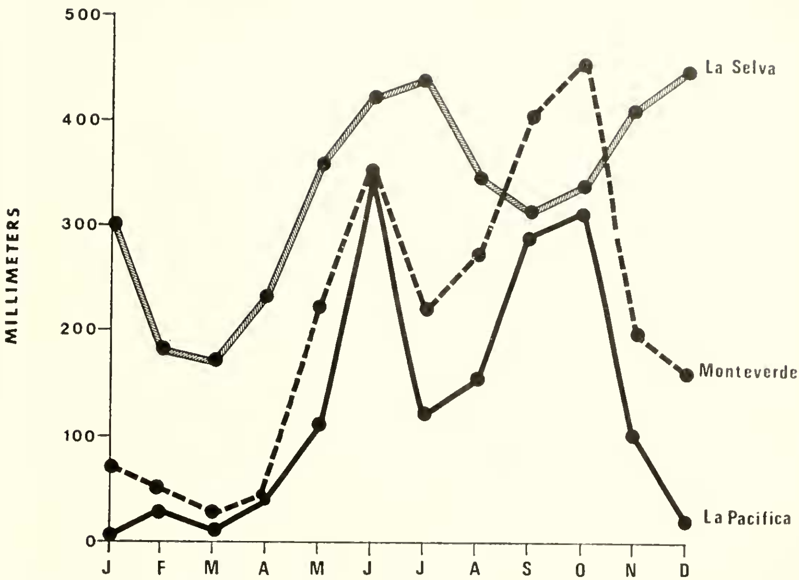

FIG. 1.—Rainfall at three sites in Costa Rica.

Usually, nets were left in place until about 2200 hours. The trap was left out all night, and checked at about 2100 and again at about 0600 hours the next morning; its effectiveness sometimes was reduced by heavy rains. Typically eight to twelve nets were set diagonally across trails. Often nets were set end to end; equally often, they were spaced with one to three empty net-lengths between. A total of 261 net-nights were tallied for La Selva, and 189 for Monteverde. The trap was set for 76 nights at La Selva, 58 nights at Monteverde (Table 2). At COMELCO a few nets were used in special situations: two or three nets each, once a month, at a small cave below a large waterfall; over water at a ford; and two nets at the entrance to the Cueva del Tigre, near the Palo Verde Field Station. The Palo Verde netting effort was abandoned after *Pteronotus parnellii* ceased using the cave. At La Pacifica the trap was set occasionally, mostly during the dry season. On a few dates during the dry season, two to four nets were set over water at the nearby Río Abangares and Río Congo.

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TABLE 2.—Species Diversity at Three Sites in Costa Rica, Comparing Results from Two Sampling Techniques. La Pacifica Data from Fleming, et al., 1972.

	Method of Capture	N Nights	Total N Species Captured Net or Trap	Total N Individuals Captured	Mean N Individuals per Net-or Trap-Night	H′	J	N Species Captured by Other Methods	Total N Species Captured
La Selva: Tropical Wet Forest	nets	34	40	1208	4.21	2.69	0.68	9	58
	traps	76	38	504	6.63				
Monteverde: Premontane Moist Forest	nets	25	22	593	3.14	1.94	0.63	3	25
	traps	58	14	330	5.69				
La Pacifica: Riparian Forest	nets	42	27	964		2.07	0.63	6[1]	33[1]

[1] Includes six species captured in our study but not netted by Fleming, et al., 1972.

and M. Moss) for their warm hospitality and permission to conduct our studies on their property. T. H. Fleming generously made available to us his records of bats banded at La Selva in 1970-71 and provided a critical review of an early draft of this paper. L. de la Torre and J. Péfaur assisted in preparation of the Spanish summary.

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Results and Discussion

Distribution Among Habitats.—At La Selva bats were captured in several different habitats, as follows: primary forest, cacao groves (shaded by scattered old-growth forest trees) and second-growth forest; whereas, at Monteverde bats were captured in primary forest, undisturbed riparian forest and second-growth forest. Netting and trapping success was evaluated for the more common species in each of these habitats at each site. At La Selva, primary forest accounted for more than half of all net- and trap-nights, whereas at Monteverde second-growth forest accounted for more than half.

Relative overall abundance in the habitats is indicated by numbers of bats caught per net-night and trap-night (Table 3). Trapping success at La Selva and both trapping and netting success at Monteverde were highest in second-growth forest. Netting success at La Selva was highest in cacao, primarily because of the large numbers of *Carollia* taken there. Preliminary examination of seedloads carried by *Carollia* shows that *Piper*, a common early successional plant along trails in disturbed areas, was the major food item in the diet of these bats. It is hardly surprising that more bats were caught at ground level in disturbed habitats, simply because the canopy is lower and thus ground level nets sample a higher percentage of the flyway area through which bats must pass. Furthermore, disturbed habitats usually contain concentrations of *Piper*, *Cecropia*, *Solanum*, and other plants frequently used by frugivorous bats; whereas food sources in the primary forest, though numerous

Table 3.—Mean No. of Bats Captured Per Net-Night and Trap-Night in Three Habitats at Two Costa Rican Sites.

LA SELVA			MONTEVERDE		
	net	*trap*		*net*	*trap*
Primary Forest	3.92	5.82	Primary Forest	1.93	5.33
Cacao	5.01	7.63	Riparian Forest	2.65	3.45
Second-growth	3.74	10.33	Second-growth	3.85	6.27

and diverse, have a patchy distribution, both horizontally and vertically. It should not be concluded, however, that the actual density of bats is greater in disturbed forest, as opposed to primary forest; our observations lead us to suspect that the converse is true at these two sites.

Foliage-gleaning bats of the genera *Micronycteris, Trachops, Mimon, Tonatia* and *Vampyrum* were taken mainly in primary forest. This is surprising because the large arthropods and small vertebrates on which they feed appear to be quite common in cacao and second-growth. Other species for which data are adequate seem to be equally distributed in all three habitats.

At Monteverde, bats of different species seemed to be evenly distributed among the habitats, except that 91 percent of the *Myotis keaysi* captured were in second-growth.

Movements.—Two-hundred and fifty-one bats of 22 species were recaptured at La Selva (23.9%) and 93 bats of ten species at Monteverde (15.9%). This rather substantial difference in recapture percentage is probably a function of both the relatively spotty netting coverage at Monteverde and the difference in species composition of the bat faunas at the two sites, i.e., *Carollia brevicauda* and *C. castanea*, with their relatively high recapture rates, were the most common bats at La Selva, whereas *Sturnira ludovici* and *Myotis keaysi*, the two most common species at Monteverde, had lower recapture rates. At La Selva recapture rates ranged from a high of 75 percent for *Mimon cozumelae* to a low of 1.8 percent for *Furipterus horrens* (Table 4). At Monteverde rates varied between 36.4 percent for *Carollia brevicauda* and 3.8 percent for *Myotis nigricans* (Table 5). The species with five or more individuals recaptured (Tables 4 and 5) were subjected to chi-square tests, separately for the two localities, and were found to differ significantly in percentages of recaptured individuals ($X^2 = 16.29$, $0.05 > P > 0.02$ for La Selva; $X^2 = 10.73$, $P < 0.001$ for Monteverde). Though the two sites shared relatively few species, it is interesting to note that only in the case of one species, *Carollia brevicauda*, were the recapture percentages of similar values. For *Glossophaga commissarisi, Pteronotus parnellii* and *Myotis nigricans* there were wide discrepancies.

Mean recapture distances at La Selva (for species with three or more recaptures) ranged from 750 m (*Desmodus rotundus*) to 133 m (*Myotis nigricans*), whereas at Monteverde they ranged from 650 m (*Glossophaga commissarisi*) to 163 m (*Artibeus toltecus*). Mean recapture time intervals for La Selva ranged from a high of 281.3 days for *Mimon crenulatum* to a low of 49.4 days for *Mimon cozumelae*. At Monteverde the high was only 104.8 days (*Vampyrops vittatus*), the low 59.3 days (both *Glossophaga commissarisi* and *Artibeus toltecus*). At La Selva, mean recapture distances, as well as mean recapture intervals, differed significantly among the species when subjected to an analysis of variance ($F=2.26$ and 2.17; $P<0.01$). At Monteverde the same was true ($F=3.13$, $P<0.01$; $F=2.18$, $P=0.05$). However, the grand mean recapture distance for La Selva was found not to differ significantly from the corresponding distance at Monteverde ($t=0.37$; $P>0.5$). Likewise the grand mean recapture time did not differ significantly between La Selva and Monteverde ($t=1.33$; $P=0.2$). A Mann-Whitney U-test gave similar results ($U=39$ with critical value of 17; $P>0.05$ for distance; $U=79$ with critical value of 17; $P>0.05$ for time interval). For the four species common to the two sites, mean recapture distance and time values were disparate, excepting mean recapture time of *Carollia brevicauda* (Tables 4 and 5), which differed by only two days at the two sites.

The significantly higher recapture rate at La Selva (23.9%, as opposed to 15.9% for Monteverde and 12.9% for La Pacifica) suggests that the behavior of the bats must expose them to nets and traps more frequently at La Selva than at the other sites. This behavior may be related in part to the year-round availability and diversity of food sources at La Selva. Thus, the less seasonal climate at La Selva may necessitate fewer seasonal movements there than at Monteverde or La Pacifica, resulting in fewer individual bats leaving the study area to search for food. If this is true, one would expect a higher number of multiple recaptures at La Selva than at Monteverde and La Pacifica. Such proved to be the case, as the average numbers of times recaptured was 1.55 at La Selva, 1.38 at Monteverde, and 1.35 at La Pacifica.

From the conclusions of Fleming, et al. (1972), or on the basis of time required to move, one would predict mean recapture percentage (and perhaps also mean recapture time interval) to be inversely proportional to mean recapture distance. Further, we would expect to find large negative correlation coefficients when the grand means from Tables 4 and 5 are subjected to correlation analysis (except for recapture distance and recapture time, which should be positively correlated). Such is not the case; none is significant at the 5 percent level at either La Selva or Monteverde. Therefore, we cannot lend support to the hypothesis of Fleming, et al. (1972), that recapture percentages should be inversely related to mean recapture distance, based on these data. The mean recapture distances found in this study are in many cases different from those found for the same or related species by Fleming, et al. (1972) or Heithaus, et al. (1975) at La Pacifica. Although these differences undoubtedly result partly from differences in the design of the studies (for example, in widely spaced *vs.* closely adjacent net sites, and in use of the bat trap), it is possible that they also reflect real behavioral differences among populations of the same or related species at the three sites, which in turn reflect differences in

TABLE 4.—Capture-Recapture Data on Bats from La Selva. (Means are given in parentheses below observed ranges)

	Total *N* Banded	*N* Recaptured At least Once	Percent Recaptured	Mean Times Recaptured	Total *N* Recaptured	Recapture Distance (m)	Recapture Interval (days)	Longest Multiple Recapture Interval (days)
Saccopteryx bilineata	18	2	11.1	1.00	2	120-1000 (560)	140-156 (148)	...
**Trachops cirrhosus*	29	5	17.2	1.00	5	0-660 (212)	1-184 (93)	...
Tonatia bidens	14	1	7.1	1.00	1	...	...	
Tonatia minuta	6	1	16.7	1.00	1	(100)	(6)	...
**Mimon cozumelae*	8	6	75.0	1.17	7	100-830 (299)	3-103 (49.4)	143
**Mimon crenulatum*	5	3	60.0	1.00	3	170-820 (553)	270-291 (281.3)	...
**Glossophaga commissarisi*	48	10	20.8	1.20	12	80-810 (428)	9-159 (83.2)	241
**Glossophaga soricina*	14	3	21.4	1.00	3	0-550 (340)	72-133 (97.3)	...
**Carollia brevicauda*	276	92	34.1	1.46	147	0-1230 (259)	6-305 (69.7)	346
**Carollia castanea*	171	63	36.8	1.37	116	0-1050 (280)	1-304 (88.5)	304
**Carollia perspicillata*	80	13	16.3	1.08	14	50-770 (310)	37-321 (104.9)	321
**Artibeus phaeotis*	92	16	17.4	1.31	21	0-1230 (435)	1-266 (101.3)	305

Artibeus jamaicensis	76	2	2.8	1.00	2	250-450 (350)	30-47 (38)	—
Artibeus literatus	16	1	6.3	1.00	1	(150)	(20)	—
Vampyressa pusilla	23	1	4.4	1.00	1	(820)	(15)	
Ectophylla alba	27	1	3.7	1.00	1	(100)	(7)	—
**Desmodus rotundus*	8	4	50.0	1.25	5	180-1050 (750)	38-146 (101.7)	—
**Pteronotus parnellii*	22	3	13.6	1.00	3	50-390 (257)	7-235 (86.3)	—
Furipterus horreus	57	1	1.8	1.00	1	(100)	(6)	—
**Myotis elegans*	12	5	41.7	1.60	8	0-510 (168)	3-122 (62.1)	219
**Myotis riparius*	43	15	34.9	2.13	32	0-630 (230)	1-180 (75.8)	278
**Myotis nigricans*	9	2	22.2	1.50	3	100-180 (133)	86-221 (139.3)	—
TOTALS	1049	251			389			
GRAND MEANS(*)			23.9	1.55		332.3	102.4	

* Only these species are included in Grand Means.

TABLE 5.—Capture-Recapture Data on Bats from Monteverde. (Means are given in parentheses below observed ranges)

	Total *N* Banded	*N* Recaptured At least Once	Percent Recaptured	Mean Times Recaptured	Total *N* Recaptured	Recapture Distance (m)	Recapture Interval (days)	Longest Multiple Recapture Interval (days)
Anoura geoffroyi	10	2	20.0	1.00	2	1000-1500 (1250)	75-269 (172)	......
*Glossophaga commissarisi	33	4	12.1	1.00	4	0-1200 (650)	17-135 (59.3)	......
Choeroniscus godmani	3	1	33.3	1.00	1	(350)	(43)	......
*Carollia brevicauda	33	12	36.4	1.42	17	0-1200 (412)	1-149 (67.5)	148
*Sturnira ludovici	180	38	21.1	1.24	47	0-1000 (280)	1-305 (103.2)	305
*Artibeus toltecus	100	7	7.0	1.14	8	0-1000 (163)	3-150 (59.3)	162
*Vampyrops vittatus	16	3	18.8	1.00	3	0-700 (391)	80-149 (104.8)	......
Pteronotus parnellii	5	1	20.0	1.00	1	(800)	(71)	......
*Myotis keaysi	178	24	13.5	1.83	44	0-1450 (196)	28-118 (59.5)	278
Myotis nigricans	26	1	3.8	1.00	1	0	(31)	......
TOTALS	584	93			128			
GRAND MEANS*			15.9	1.38		193.4	75.6	

* Only these species are included in Grand Means.

temporal and spatial distribution of food resources. For example, at La Pacifica bats tend to fly over the river and riparian forest during the dry season because food resources become concentrated there during those months. No such restriction is placed on flight paths at La Selva. The contrasting results from the three studies seem to point out that great caution must be exercised in applying generalizations from data taken in one habitat to a second, strikingly different habitat, especially when the study designs differ.

Among the species most commonly encountered in this study, four (*Carollia brevicauda, C. castanea, Myotis riparius,* and *M. elegans*) had short recapture distances, suggesting relatively small activity ranges, whereas *Trachops cirrhosus, Glossophaga commissarisi, Carollia perspicillata, Sturnira ludovici, Artibeus phaeotis, A. toltecus* and *Myotis keaysi* had comparatively long recapture distances, suggesting relatively large ranges.

Somewhat similar range sizes were found by Fleming, et al. (1972) and Heithaus, et al. (1975) from study of La Pacifica data, and by LaVal (1970) at La Pacifica and the Osa Peninsula, at least as far as the few species common to all three studies are concerned. However, most of our recapture rates were considerably higher than the ones previously reported. There are several reasons for this: Fleming, et al. (1972) and LaVal (1970) used the same netting sites repeatedly, whereas in this study we rarely used the same site twice. As suggested by LaVal (1970), bats are less likely to be caught at the original capture site than at some alternative site. LaVal's 1970 study suffered from this shortcoming and was restricted to six nights of netting at each of two sites. In the present study, the trap scored a higher percentage of recaptures than the nets, ranging up to 100 percent recaptures one night at La Selva. The mean recapture percentage for trapping was 6.3 percent higher than for netting at La Selva and 1.6 percent higher at Monteverde. Furthermore, among those bats recaptured, 4.6 percent more (La Selva) and 18.1 percent more (Monteverde) were recaptured in the trap than originally captured in it. In other words, more bats originally caught in the nets were recaptured in the trap than vice versa.

If size of foraging range in bats increases in direct proportion to body size (as often the case in vertebrates), then one might expect a significant positive correlation between mean recapture distance and length of forearm or weight. Heithaus, et al. (1975) found a suggestively large positive correlation ($r=0.75$) at La Pacifica, but it was not significant. In this study correlation coefficients for mean recapture distance and forearm length were smaller at Monteverde ($r=0.57$, $P>0.05$) and much smaller at La Selva ($r=-0.09$, $P>0.05$). It seems probable to us that increasing diversity in food habits and foraging behavior will lead to decreasing correlation between range and body size, as has been observed at La Selva. Whatever the pattern, the problem deserves further study.

The exceptionally high recapture rate and high mean recapture distances of the two species of *Mimon*, which are probably foliage-gleaning insectivores, are unexplainable given present knowledge, but must reflect some unusual behavioral traits. Extremely low recapture rates in several species, especially *Tonatia bidens*, *Artibeus jamaicensis*, *A. lituratus*, *Vampyressa pusilla*, *Ectophylla alba* and *Myotis nigricans* (Monteverde only) suggest that these species either may be nomadic or else may be unusually proficient at avoiding mist nets and traps on their second encounter. The recapture percentage of *Furipterus horrens* was lowest of all, but most of the individuals were caught by hand in a log. None was taken in mist nets, and few were caught in the trap.

At La Selva, of 79 bats banded by T. Fleming in November and December 1970 and January and February 1971, 14 (17.7%) were recaptured at least once in this study, compared with our recapture rate of 23.9 percent for the bats banded in this study. The recapture rate for Fleming's bats would have been much higher had it not been for the large numbers of *Artibeus jamaicensis* and *Desmodus rotundus* he banded. Only two *Desmodus* and no *Artibeus* were recaptured. The recaptured bats were still within several hundred meters of the original banding site after three years.

On 30 December 1975, on a brief visit to Monteverde, eight nets were erected at a site in undisturbed forest. Four (11.8%) out of 34 bats netted were recaptures, similar to the original overall recapture rate (Table 5) of 15.9 percent. These results suggest that many of the bats banded in 1973 still survive in the same general area after nearly three years.

Community Structure.—Data on the numbers of species encountered and numbers of individuals netted or trapped are compared in Table 2 with similar data from La Pacifica. The diversity in these three communities is compared using an index of species diversity based on information theory, $H' = -\Sigma p_i \log_e p_i$, and the "eveness" or equitability component of diversity, $J = H'/H_{max}$ (Pielou, 1969). Capture-rate is given for La Selva and Monteverde only.

The species composition and relative numbers of individuals in our study were augmented by use of the trap in addition to mist nets. Thus *Peropteryx kappleri*, *Rhynchonycteris naso*, *Centronycteris maximiliani*, *Micronycteris nicefori*, *M. brachyotis*, *Barticonycteris daviesi*, *Macrophyllum macrophyllum*, *Lichonycteris obscura*, *Furipterus horrens* and *Myotis elegans* were caught only in the trap (of the two means of capture) at La Selva, and *Pteronotus suapurensis* and *Myotis oxyotus* at Monteverde. Furthermore, the trap captured over 50 percent of the individuals of each of these additional species at La Selva: *Saccopteryx leptura, Pteronotus parnellii, Micronycteris megalotis, Mimon crenulatum, Choeroniscus godmani, Hylonycteris underwoodi,* and *Myotis riparius,* plus three more species at Monteverde: *Pteronotus parnellii, Micronycteris megalotis* and *Myotis keaysi.* Had the trap not been used, diversity indices calculated from these data would have been substantially lower. We believe that our indices are therefore a more accurate measure of bat diversity than previously published indices based solely on mist netting data.

The high species diversity of La Selva is clearly indicated by the high value of H'. Also, the higher J value for La Selva indicates that individuals are distributed more uniformly among the species. If animal diversity is correlated with structural diversity of the environment, then the high H' values for La Selva and the comparatively low H' values for Monteverde and La Pacifica should be reflected in high or low structural diversity. Humphrey (1975:321) outlined the causal chain for this relationship as follows: ". . . structural diversity results in diversification of food resources, permitting invasion by new species, specialization or generalization of feeding habits regulated by the resources' patchiness, and finally a decrease in niche breadth and increase in competitive exclusion." The fact that Tropical Wet Forest, as exemplified by the forest at La Selva, exhibits significantly higher structural diversity than Premontane Moist and Wet forests (Monteverde) or Tropical Dry Forest (La Pacifica) is unchallenged, to the best of our knowledge. Although the structural differences have not all been quantified, the greater structural diversity at La Selva was obvious from this study and from numerous other studies, published or in progress. The increase in bat species diversity and concomitant decrease in niche breadth is apparent not only from the diversity indices, but also from the niche matrices (Table 6) discussed below. Another indicator of differences in diversity is the fact that at La Pacifica and Monteverde most of the individuals captured belonged to 4 and 3 species (Appendix I), respectively; whereas at La Selva most belonged to 7 species. Bats of the genera *Carollia* and *Artibeus* were common at all three localities.

Niche matrices were constructed for La Selva and Monteverde following the reasoning of McNab (1971) and Fleming, et al. (1972). We used length of forearm as a crude index of body size, although weight would have been a better index if it had been available for all species. For example, *Artibeus jamaicensis* and *Pteronotus parnelli* have forearms of 64 mm and 62 mm, respectively, whereas their weights are 55 g and 24 g, so they are separated into different cells only by food habits if forearm length is the size criterion. Similarly, *Carollia brevicauda* (FA of 41 mm) is in the same cell as *Artibeus phaeotis* (FA of 39 mm) on this basis,

TABLE 6. Distribution of Bat Species by Body Size (As Estimated by Forearm Length) and Food Preferences From Three Costa Rican Localities.

	Mean Forearm Length (mm)						
	30-34	35-43	44-54	55-68	69-86	87+	TOTALS
LA SELVA							
insects-aerial	4	6	4	3			17
insects-foliage-gleaning	1	7	2	3			13
fish					1		1
flesh				1		1	2
plants-fruit	2	7	4	1	1		15
plants-pollen/nectar	4	1					5
blood				1			1
omnivore	1			1	1	1	4
TOTALS	12	21	10	10	3	2	58
cells occupied	5	4	3	6	3	2	23
MONTEVERDE							
insects-aerial	1	4	3	1			9
insects-foliage-gleaning		1					1
fish							0
flesh						1	1
plants-fruit		4	1	2			7
plants-pollen/nectar	2	2	1				5
blood							0
omnivore	1						1
TOTALS	4	11	5	3	0	1	24
cells occupied	3	4	3	2	0	1	13
LA PACIFICA							
insects-aerial	2	3	3	2			10
insects-foliage-gleaning	1	4					5
fish					1		1
flesh				1	1	1	3
plants-fruit		5	1	1	1		8
plants-pollen/nectar	1	2					3
blood				1			1
omnivore	1			1			2
TOTALS	5	14	4	6	3	1	33
cells occupied	4	4	2	5	3	1	19

but their weights are quite different (19 g *vs.* 12 g). Although the bias inherent in the use of forearm length is substantial in these and certain other cases, it does not entirely negate the value of the niche matrices and must be used until weights for the rarer species become available.

Niche matrices for La Selva, Monteverde and La Pacifica (La Pacifica data modified from Fleming, et al., 1972) are shown in Table 6. The La Pacifica matrix is augmented by the addition of 5 species caught there in the trap (that were not taken by Fleming, et al.)—*Saccopteryx leptura, Glossophaga commissarisi, Choeroniscus godmani, Hylonycteris underwoodi* and *Myotis elegans.* Also included is *Vampyrum spectrum,* a group of which roosted in a hollow tree on the bank of the Río Corobicí near La Pacifica.

The assignment of species to food categories is based on a variety of information. In this study fecal samples were collected from as many species of bats as possible. Although analysis of these samples is incomplete, the presence of insect remains or seeds suggests an insectivorous or frugivorous diet. The division of insectivores into aerial and foliage-gleaning is based on morphology, plus field observations of several species, in the present as well as past studies by LaVal. A detailed food study of one foliage-gleaner *(Micronycteris megalotis)* was carried out. The consumption of fish, flesh, and blood by some bats is well documented both in the literature and by our unpublished observations. The separation of plant-feeders into frugivores and nectarivores is based on fecal samples, morphology, and the literature. As shown by Heithaus, et al. (1975), many frugivores use pollen and nectar (at least seasonally), and at least one nectarivore *(Glossophaga soricina)* also eats fruit seasonally and probably should be regarded as an omnivore. Many other species of pollen- and nectar-feeding bats exhibit a greater degree of morphological specialization for nectarivory than *Glossophaga,* and probably they will prove to have correspondingly specialized habits (as in México; see Alvarez and Quintero, 1970). Although most of the species occurring at two or three sites are assigned to the same food category, we recognize that detailed studies of feeding behavior may establish that some species have different food habits at each of the sites.

Of the 48 cells in our matrices, 23 were occupied at La Selva, 13 at Monteverde, and 19 at La Pacifica. La Selva differed from La Pacifica primarily in the presence of more species per cell. Additionally, quite a few more species of foliage-gleaning insectivores lived at La Selva. Monteverde differed from the other localities in having fewer species per cell and in having zero or only one cell for foliage-gleaners, piscivores, carnivores, sanguinivores, and omnivores. Among pollen- and nectar-feeders Monteverde had as many species as the other sites and more occupied cells. At all three sites, greatest occupancy is in the 35-43 mm insect-eating cells, followed by the 35-43 mm plant-eating cells, suggesting either a finer degree of niche separation among these species or simply a greater variety of potential niches available to bats of that size range. Although it seems amazing that 13 species of insectivorous bats can co-exist in the 35-43 mm cell at La Selva, most of these species have strikingly different morphologies, and, insofar as observed, they differ substantially in feeding behavior, especially in terms of vertical stratification. However, certain species pairs, such

TABLE 7. Reproductive Data on Females of Some Species of Costa Rican Bats. Numbers represent number pregnant/number examined. Abbreviations: L, Lactating; PL, Postlactating; J, Juvenile; SA, Subadult. Locations are: LS, La Selva; M, Monteverde; G, Guanacaste (La Pacifica, COMELCO, etc.); ALL, all three sites.

Species	Site	F	M	A	M	J	J	A	S	O	N	D	J	F	M
Rhynchonycteris naso	G	0/6	3/3	2/2 4L 3J	1/1							0/1	0/1J		
Saccopteryx leptura	LS	0/1	0/1					0/1							
Saccopteryx bilineata	LS		1/3	1/1	1/1				1/1			1/2		0/1	
Noctilio labialis	G	10/40		1/1				1/1 (LS)							
Pteronotus parnellii	LS, G		9/11	1/1	1/3 2L		0/2 17SA	0/1	0/1	0/15	0/14	0/23	17/19		
Micronycteris megalotis	ALL			2/2	1L		1PL 1J 1SA	1SA	1SA	0/1		0/1	0/1	0/1	
Macrophyllum macrophyllum	LS, G		1/1		1/1		0/1 1J			0/1					
Tonatia bidens	LS						0/2 1PL	0/1 1J		0/2					
Tonatia minuta	LS			1/2				0/1						1/1	
Mimon cozumelae	LS			3/3			1J	1L 1SA							
Mimon crenulatum	LS			1/1										0/2	
Trachops cirrhosus	LS			5/6			0/5 10J 1SA			0/1					
Vampyrum spectrum	LS						0/1			0/1				0/1	
Glossophaga soricina	LS		1/1	0/1 1L			0/3			1/1				2/2	

Lonchophylla robusta	LS				1/1			1/1 1L 1SA		1/2			1L	1/2 1PL 1J	
Choeroniscus godmani	ALL	1/1		0/2	0/1		0/1			0/1		0/1	1/2	1/1	
Hylonycteris underwoodi	MV,LS			1/1	0/3		1PL	1/2	0/2	1/2	1/1		1/4	1/3	1/1
Vampyrops helleri	LS							2/3 1SA			2J		0/3 1PL	0/1 1SA	
Vampyrops vittatus	MV		3/3	0/1			1J	2SA	1PL 1SA	1SA					
Vampyrodes major	LS	1/1													
Uroderma bilobatum	LS			0/1			2/2	0/1 1PL	1L 1PL	1J			1/2 1PL	2/2	
Artibeus lituratus	LS			1/1	0/1		1/1	0/1 1L 1J	1L	0/1	1/1 1L				
Artibeus watsoni	LS			1/1			1J								
Vampyressa pusilla	LS	1/1		1/1	2L		1/2 1L	1/2	2/2 2L	1J				0/3	
Ectophylla alba	LS		1L					1/1	1PL		1PL			1/2	
Desmodus rotundus	LS	0/1						0/1 2SA	1SA			0/1		1PL	
Thyroptera tricolor	MV					1J									
Myotis elegans	LS			1/1		1SA	1SA	0/1					0/2	0/1	
Myotis riparius	LS			4/5 1L	1/2 3L		1/5 1SA	0/3	0/7 1SA	0/1 3SA	0/1	0/7		0/2	
Molossus ater	G	1/4	2/2												
Molossus bondae	LS							2/3			0/5 2SA		1/1	0/2	
Molossus pretiosus	G				5/5		2/3 4SA			5/12 1PL 5SA	0/2				

as *Myotis riparius* and *M. elegans,* as well as *Micronycteris brachyotis* and *M. nicefori,* are so similar morphologically that a careful study of their food habits and feeding behavior is needed to determine how their niche requirements might differ. That similar-sized bats do indeed differ in food habits, at least in the relative amounts of the different species of plants utilized, has been established at La Pacifica (Heithaus, et al., 1975), has been suggested for a number of other Costa Rican species (Howell and Burch, 1974), and will probably also prove to be the case at Monteverde and La Selva, as suggested by the preliminary examination of seeds collected from feces of frugivorous bats in this study.

Reproduction.—Only three of the four different reproductive patterns described by Fleming, et al. (1972) were observed in this study, at least among adequately sampled species.

Seasonally monestrous: Pteronotus parnellii seems to conform with this pattern, at least in Guanacaste (Table 7), as does *Myotis riparius* at La Selva.

Seasonally polyestrous: At La Selva this pattern included the three species of *Carollia* (Fig. 2), plus *Artibeus phaeotis* and *Glossophaga commissarisi* (Fig. 3). At Monteverde, *Sturnira ludovici, Artibeus toltecus,* and *Myotis keaysi* (Fig. 4) were seasonally polyestrous. Although the generalizations about bimodal birth peaks made by Fleming, et al. (1972) seem to apply to all of them (except perhaps *Myotis keaysi*) the actual timing of the peaks varies one to three months among the different species, perhaps in response to different fruiting and flowering periods among their food plants. All species seem to exhibit minimum reproductive activity (no pregnancies) late in the wet season, from October to early January. In *Carollia brevicauda* at La Selva this nonreproductive period is relatively brief, but in *Sturnira ludovici* and *Artibeus toltecus,* in the dryer climate of Monteverde, it is relatively long. Although no data were obtained for the latter two species during February of the study period, examination of bats captured on 10 February 1977 revealed that 21% (6 of 28) female *S. indovici* and 50% (13 of 26) female *A. toltecus* were pregnant.

Table 7 suggests that the seasonally polyestrous pattern is common among the frugivorous stenodermine and the nectarivorous glossophagine bats, but less frequent in the foliage-gleaning phyllostomine bats and molossids. Nine species of phyllostomatid bats south of the equator in Brazil (Taddei, 1976) were also seasonally polyestrous.

Year-round activity: Tentatively, *Molossus sinaloae* (Fig. 3) at La Selva has been placed in this category, but there is a three-month gap in our data. Occurrence of pregnant females before the gap and the capture of juveniles following the gap suggest that there is some reproductive activity throughout the year; but most

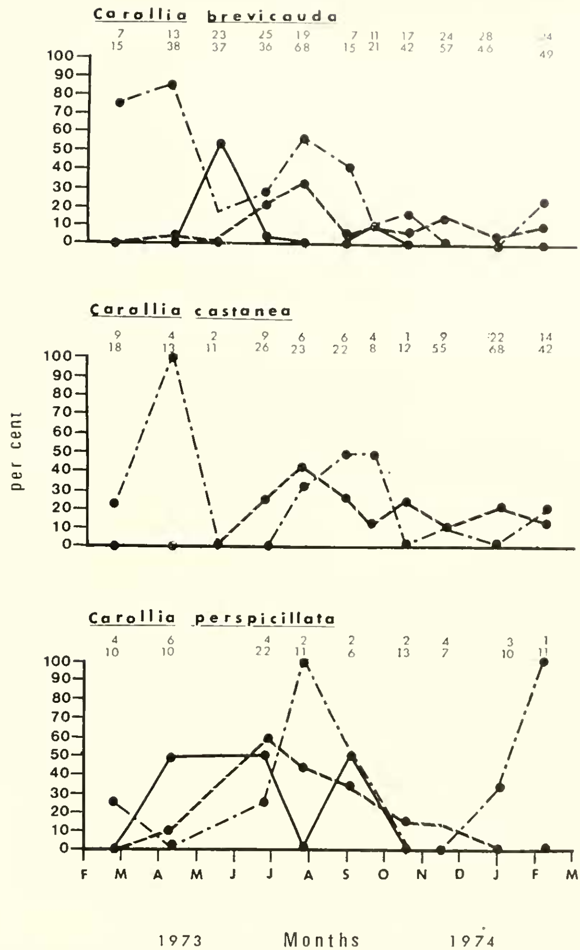

FIG. 2.—Indicators of reproductive cycle timing of three species of *Carollia* at La Selva, Costa Rica. The "dash-dot" line indicates percentages of adult females that were pregnant. The solid line indicates percentages of adult females that were lactating. The "slanted-dash" line indicates percentages of all bats captured that were juveniles. The lower of the small figures below the species name is the total number of bats caught each month. The upper of the small figures is the number of adult females captured each month.

pregnancies were in the late dry season and early wet season when females of most other species of bats we examined were also pregnant.

These reproductive cycles are related to fruiting, flowering, and insect abundance (Fleming, et al., 1972) and will be dealt with in a future paper (LaVal and Fitch, MS).

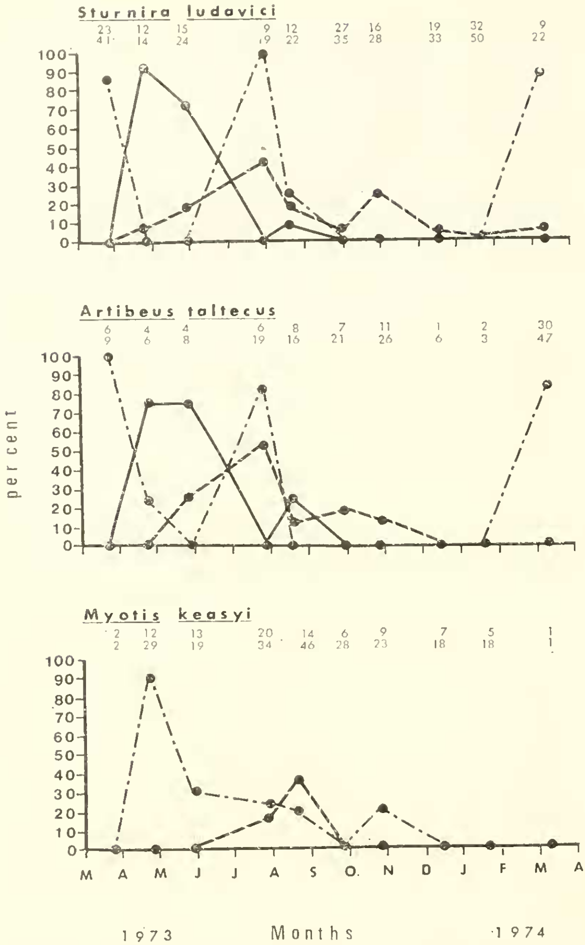

Fig. 3.—Indicators of reproductive cycle timing of three species of bats at La Selva, Costa Rica. See explanation in caption for Fig. 2.

Summary

Harp traps and mist nets were used to sample bats at monthly intervals for one year at three sites of contrasting climate and natural vegetation in Costa Rica. Bats were examined, banded, and released in order to document community structure, distribution among habitats, movements, and reproductive strategies.

Community structure at the Tropical Wet Forest site is characterized by high species diversity ($H'=2.69$) and high occupancy rate (48%) of niche matrices (body size plotted against food preferences), with as many as 7 species per cell. At the Tropical Dry Forest site species diversity is lower ($H'=2.07$), as is the occu-

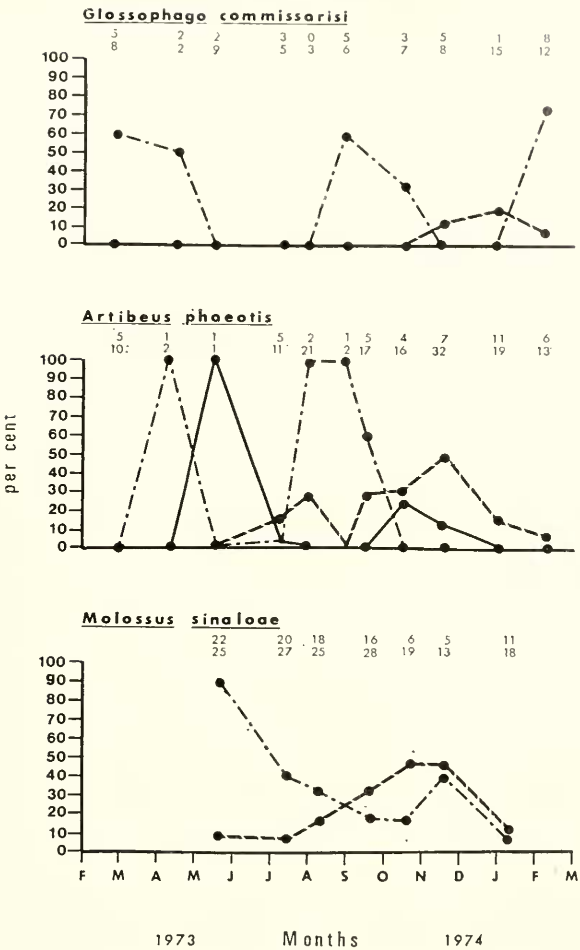

FIG. 4.—Indicators of reproductive cycle timing of three species of bats at Monteverde, Costa Rica. See explanation in caption for Fig. 2.

pancy rate (40%), with no more than 5 species per cell. At the Premontane Moist Forest site, both species diversity ($H'=1.94$), and occupancy rate (27%), are even lower, with no more than 4 species per cell.

Bats were unequally distributed among habitats at the two sites where pertinent data were collected. At La Selva trap results showed nearly twice the catch-rate in second-growth, as compared to primary forest, whereas net results at the two sites differed little. At Monteverde trap data showed a somewhat greater catch-rate in second-growth forest, whereas netting results gave much higher catch-rates in second-growth than in primary forest.

Mean movements of banded bats were high at La Selva (332 m), lower at La Pacifica (258 m), and still lower at Monteverde (193 m). As there is no reason to believe some bats banded in this project did not move beyond the radius of the study areas during the study period, mean distances moved are minimal. Because this sequence is the reverse of the predicted sequence of mean distances moved, it is not possible to relate them to food habits and activity ranges in any meaningful way based on our data. However, recapture rates suggested that activity ranges are smaller at La Selva (recapture rate of 23.9%), as compared to Monteverde (15.9%) and La Pacifica (12.9%).

All bats in this study except *Molossus sinaloae* at La Selva, were found to have seasonal reproduction, with the shorter, more sharply delineated reproductive seasons characteristic of La Pacifica, with its relatively brief wet season; longer reproductive seasons, as evidenced by polyestry, were more typical of La Selva, with its very long wet season. Monteverde, with its wet season of intermediate length, was more like La Pacifica than it was like La Selva, in terms of reproductive cycles.

Resúmen

Trampas de arpa y redes de nylon fueron usadas para obtener murciélagos una vez al mes durante un año en tres lugares de clima y vegetación diferentes en Costa Rica. Los murciélagos fueron procesados, marcados, y soltados para documentar el movimiento, distribución ecológica, estructura de comunidad, y estratégias reproductivas.

El area de forrajear, indicada por medio de las distancias de recaptura, fue más grande en lugares de bosque muy húmedo ("Wet Forest"). En los tres sitios, las areas de forrajear de las diversas especies variaron en amplitud.

El mejor resultado se obturo con las redes en las plantaciones viejas de cacao en lugar del bosque muy húmedo, pero en el bosque montañeso ("Premontane Moist Forest") el resultado fue mejor que en los bosques secundarios. Con las trampas, el resultado fue mejor en el bosque secundario en dos lugares.

La diversidad de la comunidad indicado por H' fue mucho mas alta en el lugar de bosque muy húmedo. El número de especies en el sitio de bosque muy húmedo (58) fue casi el doble al de los otros dos sitios. Las matrices de los nichos ("niche matrices") basados en los tres sitios indicaron que 23 células fueron ocupadas en el sitio de bosque muy húmedo, solamente 13 en el sitio de bosque montañeso y 19 en el sitio de bosque seco ("Dry Forest").

Tres modelos de reproducción fueron observados en este estudio. Pocos murciélagos insectívoros fueron "monoestros"; en cam-

bio, la mayor parte de los murciélagos frugívoros y nectarívoros y unas pocas especies insectívoros fueron "poliestros." Una de las especies insectívoras parece estar activa reproductivamente todo el año.

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APPENDIX 1: Summary Data on 78 Species of Bats from Three Localities in Costa Rica

Species	mean forearm length (mm)	mean weight (g)	Numbers of individuals captured			Food[1]
			La Selva	Monteverde	Guanacaste	
Rhynchonycteris naso	37.3	4.1	7		40	IA
Saccopteryx bilineata	45.2	7.6	17		12	IA
Saccopteryx leptura	40		7		1	IA
Peropteryx kappleri	48	16	1			IA
Centronycteris maximiliani	43.7	5	4			IA
Balantiopteryx plicata	41				1	IA
Noctilio labialis	65.0	37.8	1		44	IA
Noctilio leporinus	82				25	F
Pteronotus davyi	47.5				10	IA
Pteronotus suapurensis	54.4	14.6		2	5	IA
Pteronotus parnellii	61.2	23.7	25	7	269	IA
Pteronotus personata	47				3	IA
Micronycteris brachyotis	38	9.4	3		5	IFG
Micronycteris hirsuta	42.3	14.7	4		1	IFG
Micronycteris megalotis	34.2	6.7	21	13	3	IFG
Micronycteris minuta	34.8	9	1			IFG
Micronycteris nicefori	37.6	10.2	6			IFG
Micronycteris schmidtorum	35		1		1	IFG
Barticonycteris daviesi	56.2		1			IFG
Lonchorhina aurita	50				1	IFG
Macrophyllum macrophyllum	35		3		3	IFG
Tonatia bidens	57.5	31.8	15			IFG
Tonatia minuta	35.2	7.4	8			IFG
Tonatia sylvicola	52		1			IFG
Mimon crenulatum	50.3	15.0	10			IFG
Mimon cozumelae	57.5	25.9	16			IFG
Phyllostomus discolor	64		1		7	O
Phyllostomus hastatus	90		1			O
Phylloderma stenops	77		1			O
Trachops cirrhosus	61	32.3	35		2	F
Vampyrum spectrum	107.7	166.0	4		4	F
Glossophaga commissarisi	34.5	9.3	81	34	10	PN
Glossophaga soricina	34.0	10.5	23	6	51	O
Lonchophylla robusta	43.3	16.3	12			PN
Anoura cultrata	43.6			1		PN
Anoura geoffroyi	42.5	15.2		13		PN
Choeroniscus godmani	32.9	7.9	3	8	5	PN
Hylonycteris underwoodi	33.3	8.0	15	7	3	PN
Lichonycteris obscura	32.4	7.0	3			PN
Carollia brevicauda	41.3	18.5	461	53	75	PF
Carollia castanea	36.5	13.8	302			PF
Carollia perspicillata	44.9	22.5	101			PF
Sturnira lilium	40			2	22	PF
Sturnira ludovici	42.4	19.2	1	287		PF
Sturnira mordax	48.1	26.9		8		PF
Uroderma bilobatum	43.9	19.6	17		1	PF
Vampyrops helleri	39.8	15.4	16			PF
Vampyrops vittatus	63.4	54.7		23		PF
Vampyrodes major	53.1	32.8	1			PF

Vampyressa nymphaea	37.7		2			PF
Vampyressa pusilla	31.9	8.2	27			PF
Chiroderma villosum	46		1		1	PF
Ectophylla alba	28.1	5.6	38			PF
Artibeus jamaicensis	64.2	54.9	111		24	PF
Artibeus lituratus	66.2	63.8	16	4		PF
Artibeus phaeotis	38.8	12.4	133		5	PF
Artibeus toltecus	40.6	15.3		161		PF
Artibeus watsoni	39		4			PF
Enchisthenes harti	40.1	15		1		PF
Desmodus rotundus	59		29			B
Furipterus horrens	34.3	3.3	59			IA
Thyroptera tricolor	35			1		IA
Myotis albescens	36.3	6.3	7			IA
Myotis elegans	33.0	4.0	20		4	IA
Myotis keaysi	36.3	5.0		226		IA
Myotis nigricans	35.0	4.7	14	40		IA
Myotis oxyotus	40.7			2		IA
Myotis riparius	35.7	5.3	78	4		IA
Eptesicus andinus	44.2		1	1		IA
Eptesicus furinalis	38.8		1		2	IA
Rhogeessa tumida	29.6		1		9	IA
Lasiurus ega	45.2	11		1		IA
Molossops greenhalli	♂39.4 ♀36.9				3	IA
Molossus ater	48				6	IA
Molossus bondae	♂40.7 ♀39.2	22.9 16.8	17			IA
Molossus molossus	35				7	IA
Molossus pretiosus	♂44.9 ♀43.8	29.9 24.3			47	IA
Molossus sinaloae	♂48.8 ♀47.2	28.7 23.1	76			IA

[1] Food includes: IA, insects—aerial feeders; IFG, insects—foliage-gleaners; PF, plants—fruit; PN, plants—pollen and nectar; F, flesh or fish; O, omnivore; B, blood.